Journal of Vertebrate Paleontology 30(2):458–466, March 2010

ARTICLE

SENSITIVITY ANALYSIS IN EVOLUTIONARY ROBOTIC SIMULATIONS OF BIPEDAL DINOSAUR RUNNING

KARL T. BATES,*[,1] PHILLIP L. MANNING,[2,3] LEE MARGETTS,[2,4] and WILLIAM I. SELLERS[1]
[1]Faculty of Life Sciences, University of Manchester, Stopford Building, Oxford Road, Manchester M13 9PL, U.K., karl.bates@postgrad.manchester.ac.uk, william.sellers@manchester.ac.uk;
[2]School of Earth, Atmospheric and Environmental Science, University of Manchester, Williamson Building, Oxford Road, Manchester M13 9PL, U.K.;
[3]The Manchester Museum, University of Manchester, Oxford Road, Manchester M13 9PL, U.K. phil.manning@manchester.ac.uk;
[4]Research Computing, University of Manchester, Oxford Road, Manchester, U.K., lee.margetts@manchester.ac.uk

ABSTRACT—Constructing musculoskeletal models of extinct vertebrates requires subjective assumptions about soft tissue parameters rarely preserved in the fossil record. Despite these necessary assumptions about fundamental input values, paleobiologists rarely perform objective tests of best-estimate models before reaching conclusions based on predicted results. The extent to which lack of knowledge on soft tissue anatomy limits the accuracy of running speed estimates of extinct dinosaurs is therefore poorly understood. In this study, a sensitivity analysis is performed on an evolutionary robotics model of the non-avian theropod dinosaur *Allosaurus*, used previously to estimate maximum running speed in this extinct animal. A range of muscle parameters were varied over the range observed in extant vertebrates, whereas mass-related parameters were altered across the range of published estimates for *Allosaurus.* Muscle parameters have a linear relationship with maximum running speed, whereas surprisingly total body mass and torso center of mass have little effect. Muscle force values produced the greatest range in predicted running speeds (4.5–10.7 m/s) and stride lengths (4–5.8 m) in the sensitivity analysis, equating to 65.9% and 30.7% variation about the original 'best-estimate' prediction, a relatively high potential margin of error. These results highlight the importance of sensitivity analyses in biomechanical modeling of extinct taxa, particularly where values for soft tissues parameters are not tightly constrained. The current range in plausible values for soft tissue properties makes a robust quantitative assessment of behavioral ecology and species interactions in dinosaurian communities extremely difficult.

INTRODUCTION

Mathematical-computational modeling is an accepted approach to testing form-function relationships in extinct vertebrates. High-performance computing has become increasingly accessible to paleobiologists and provides the facility to rapidly solve the complex chain of equations that describe the mechanics and energetics of three-dimensional (3D) motion in jointed musculoskeletal systems. Computational methods are now standard for calculating the mass and inertial properties of organisms (Henderson, 1999; Henderson and Snively, 2004; Hutchinson et al., 2007; Bates et al., 2009a, 2009b) and for reconstructing the mechanical behavior (e.g., Rayfield, 2004, 2005; Richmond et al., 2005), range of motion and functional repertoire (e.g., Stevens and Parrish, 1999), and likely kinematics and energetic performance of biological structures (e.g., Sellers et al., 2004, 2005; Nagano et al., 2005). These numerical analyses have some advantages over the more traditional methods of analogy and theoretical inference because they are inherently more objective and deterministic, producing explicit quantitative predictions. Modeling methods are particularly important when suitable modern analogues are lacking for extinct taxa, because they allow the function of unique morphological structures to be reverse-engineered. Furthermore, the increased level of quantification and visualization inherent in computational methods provides a more complete understanding of the similarities and differences in form and function among taxa across space and time. Primary interpretations of mechanics and performance drawn from such analyses can subsequently be used to support secondary interpretations (or 'higher-level inferences'; Witmer, 1995) relating to behavioral ecology, clade-clade interaction, and possible selection pressures in extinction events and evolutionary radiations (Sereno, 1999).

To produce reliable biomechanical predictions, mathematical-computational procedures require a digital or numerical model that replicates the anatomy and physiology of an organism with high fidelity. Advances in computer software and digitizing technology have made the production of complex musculoskeletal models a relatively straightforward procedure (e.g., Stevens, 2002; Hutchinson et al., 2005). However, taphonomic loss and alteration of biological material means the extraction of values for skeletal and soft tissue properties from fossils is problematic and in many cases impossible. Estimations of the original material properties of bone and the geometry and physiology of soft tissues are therefore restricted to ranges exhibited by extant outgroups. Even where values are tightly constrained by an Extant Phylogenetic Bracket (EPB), input models necessarily remain best-estimate representations with an unknown level of confidence (Witmer, 1995). It is therefore best practice to perform a sensitivity analysis on biomechanical models of extinct taxa, in which uncertain best-estimate values are altered in order to observe their effects on model predictions. Sensitivity analyses have been applied in a number of recent studies (Kramer, 1999; Hutchinson, 2004a, 2004b; Sellers and Crompton, 2004; Ross

*Corresponding author.

et al., 2005; Strait et al., 2005; Hutchinson et al., 2007; Porro, 2008) but have yet to become a routine part of modeling procedure in paleobiology and biomechanics.

Sellers and Manning (2007) used multi-body dynamics and evolutionary robotic optimizations to estimate maximum running speed of the extinct non-avian theropod dinosaur *Allosaurus*. In multi-body dynamic analyses, a body is treated as a set of rigid segments acted upon by various forces and constrained by the joints between the segments. The movement of each segment is calculated by solving a large matrix of differential equations or 'equations of movement' (for a review, see Winter, 1990). To create stable running in the model, an appropriate muscle activation pattern was developed by a distributed, parallel genetic algorithm (GA) optimization system, similar to those used to spontaneously generate gait in autonomous robots (Nolfi and Floreano, 2000). The GA control system was designed to search for the muscle activation pattern that maximized performance according to specific fitness criteria, in this case maximum running speed. This system alleviates the need to subjectively infer joint kinematics or rely on extant taxa as dubious locomotor analogues. However, the accuracy of the simulated gait still ultimately relies on the bio-fidelity of the anatomical model, which necessarily includes estimation of soft tissue parameters rarely available in the fossil record. The aim of this study is to provide a confidence test of the maximum running speed of 9.4 m/s predicted for *Allosaurus* by Sellers and Manning (2007). A one-at-a-time (OAAT) sensitivity analysis (Campolongo et al., 2000) has been used to identify anatomical and physiological parameters that have greatest effect on the simulated results. In OAAT sensitivity analyses, the numerical values used as inputs to the model are treated as plausible ranges rather than best-estimates values. The model is run repeatedly and input values sampled from those ranges. OAAT sensitivity analyses have the advantage of being relatively quick to run, which is essential in the current context because the GA-based simulator is extremely slow. Monte Carlo approaches would normally be preferred because they allow the analysis of interaction between parameters as well as independent effects, but these are extraordinarily computationally expensive and so currently impractical. Altering the values of a specific parameter individually isolates its effect on gait and performance and allows the modeler to identify the input parameters that have the most significant impact on the results. In this study, a number of muscle parameters were varied over the ranges observed in extant vertebrates, whereas mass-related parameters were altered across the range of published estimates for *Allosaurus* (Table 1).

METHODS

The model and simulation procedure remained unchanged from the original study of Sellers and Manning (2007) to ensure fair and meaningful comparison of results. *Allosaurus* is represented by a 2D model with a rigid trunk, and right and left thigh, shank, and composite foot segments combining the metatarsus and foot (Fig. 1). Locomotion is driven by generalized or aggregated muscle-tendon units, specifically a single flexor and extensor across each of the three hind limb joints. The full specification for the model is included as human readable XML files as electronic supplementary material. The Open Dynamics Engine (ODE http://www.ode.org) was again used to provide the physics simulation. The muscle activation pattern was generated from our custom written genetic algorithm optimization programme (Sellers and Manning, 2007).

Simulations are computationally expensive and hence testing every input parameter with multiple re-runs would take considerable amount of time. Five parameters were selected for this study (Table 1) based on their theoretical relevance to maximum running speed in legged locomotion (Hill, 1950; Rome et al., 1988; Medler, 2002; Roberts and Scales, 2002; Hutchinson, 2004a) and the uncertainty surrounding their values for non-avian dinosaurs. Muscle force parameters used in this model (force per unit area, physiological cross-section area, and muscle mass) were linearly related so changes in any of the parameters would have exactly the same effect on the model outcome. This means that all the effects reported for varying force per unit area (FPUA) would equally apply to muscle mass or physiological cross-section area. FPUA values were tested above and below the extremes reported in the literature (Table 1) to ensure these related muscle parameters were accounted for in the analysis. Altering fiber length does not have a simple linear effect because it not only alters FPUA in our formulation but also affected contraction velocity (which is a multiple for fiber length) and the elastic properties of the system by changing tendon length. Body mass and center of mass (CM) have long been of interest to dinosaur paleobiologists and these two parameters have also been tested in the sensitivity analysis. Hind limb muscle mass remained at the original percentage of total body mass throughout the range of total body mass values tested. CM was altered by repositioning the longitudinal position (i.e., horizontal distance from hip joint) of the trunk CM, without changing the vertical position. In each case, the trunk moments of inertia were recalculated to the appriopate values. Rigorous testing of these input parameters took several months to carry out, with simulations run on a dedicated cluster of 60 processors at the University of Manchester and the supercomputer HECToR (U.K. National Supercomputing Service).

RESULTS

Stable gaits were achieved throughout the input ranges tested for FPUA, maximum contraction velocity (V_{max}), body mass, and trunk CM (Fig. 2). These remained true running gaits by kinematic definition (i.e., aerial phase present) for the full range of values for each parameter (Fig. 2). Stable locomotion was achieved with the increased fiber lengths tested, but could not be achieved when fiber lengths were lowered by 20% or more (Fig. 2).

The resulting speeds and stride lengths for each parameter have been collated in Table 2. FPUA, V_{max}, and fiber length have an approximately linear effect on running speed (Fig. 3A), with FPUA producing the greatest range in predicted speeds (Fig. 3B).

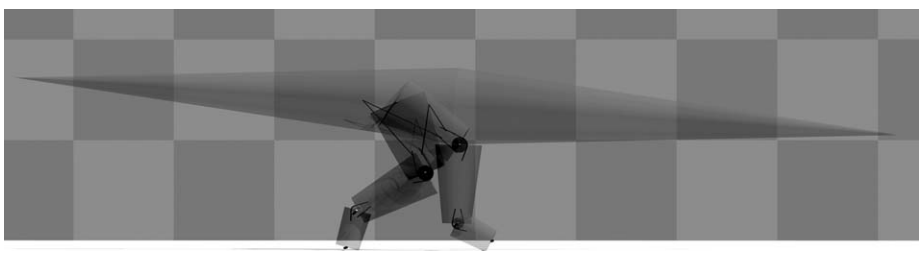

FIGURE 1. The musculoskeletal model of *Allosaurus* (Sellers and Manning, 2007). Locomotion is driven by a single aggregate flexor and extensors (grey lines) across each joint in the hind limb (spheres). Conic segments with the appropriate mass and inertial properties were used to represent the limb segments and back-to-back circular cones were used for the trunk.

TABLE 1. Numerical inputs values for OAAT sensitivity analysis sourced from literature.

Input parameter	Sellers and Manning (2007)		Range in literature		Range tested		
Muscle parameters							
Force per unit area (FPUA)	300,000 Nm^{-2}		200,000 Nm^{-2}	Weatneat, 2003	150,000–450,000 N m^{-2}		
			250,000 Nm^{-2}	Umberger et al., 2003			
			330,000 Nm^{-2}	Alexander, 2003			
			350,000 Nm^{-2}	Pierrynowski, 1995			
			360,000 Nm^{-2}	Alexander, 2003			
			400,000 Nm^{-2}	Zheng et al., 1998			
Maximum contraction velocity (V_{max})	8 s^{-1}		3–10 s^{-1}	Westneat, 2003	4–12 s^{-1}		
			4.8 s^{-1}	Umberger et al., 2003			
			12 s^{-1}	Umberger et al., 2003			
Muscle fascicle length (m)	Hip	0.52	n/a	Hutchinson, 2004	±25%	Hip	0.39–0.65 m
	Knee	0.23				Knee	0.17–0.29 m
	Ankle	0.13				Ankle	0.1–0.16 m
Mass parameters							
Body mass	1400 kg		952 kg	Paul, 1988	1100–2300 kg		
			1092 kg	Therrien and Henderson, 2007			
			1400 kg	Alexander, 1989			
			1620 kg	Christiansen and Farina, 2004			
			2300 kg	Colbert, 1962			
Trunk centre of mass (COM)	78% thigh length cranial to hip joint		7–0.78% thigh length cranial to hip joint	Hutchinson, 2004b Bates et al., 2009b	0–90% thigh length cranial to hip joint		

TABLE 2. Summary of results for OAAT sensitivity analysis.

Input parameters	Input value	Speed (m/s)	Stride length (m)	Froude number
Muscle parameters				
Force per unit area (FPUA)	150,000 Nm^{-2}	4.5	4	1.19
	187,500 Nm^{-2}	5.1	4.5	1.54
	225,000 Nm^{-2}	6.9	5.1	2.76
	262,500 Nm^{-2}	8	5.3	3.78
	337,500 Nm^{-2}	9.7	5.8	5.47
	375,000 Nm^{-2}	10	5.7	5.82
	412,500 Nm^{-2}	10.5	5.8	6.38
	450,000 Nm^{-2}	10.7	5.8	6.70
Maximum contraction velocity (V_{max})	4 s^{-1}	6.7	5.2	2.62
	6 s^{-1}	7.8	5.4	3.54
	10 s^{-1}	9.61	5.9	5.38
	12 s^{-1}	10.7	6	6.63
Muscle fascicle length	+5%	8.7	5.3	4.37
	+15%	8.2	5.3	3.95
	+25%	7.9	5.0	3.67
	−5%	9.3	5.9	5.03
	−15%	9.3	5.7	5.07
	−25%	1.1	0.4	—
Mass parameters				
Body mass	1100 kg	9.1	5.5	4.88
	1700 kg	9	5.5	4.73
	2100 kg	9	5.5	4.69
	2300 kg	9	5.5	4.74
Trunk center of mass (% thigh length cranial to hip joint)	0	9.02	4.59	4.75
	10	8.56	6.12	4.27
	20	8.81	5	4.52
	30	8.65	4.59	4.36
	40	8.8	4.96	4.51
	50	9.14	5.15	4.87
	60	8.78	4.99	4.49
	70	8.96	5.88	4.68
	90	8.84	5.65	4.55

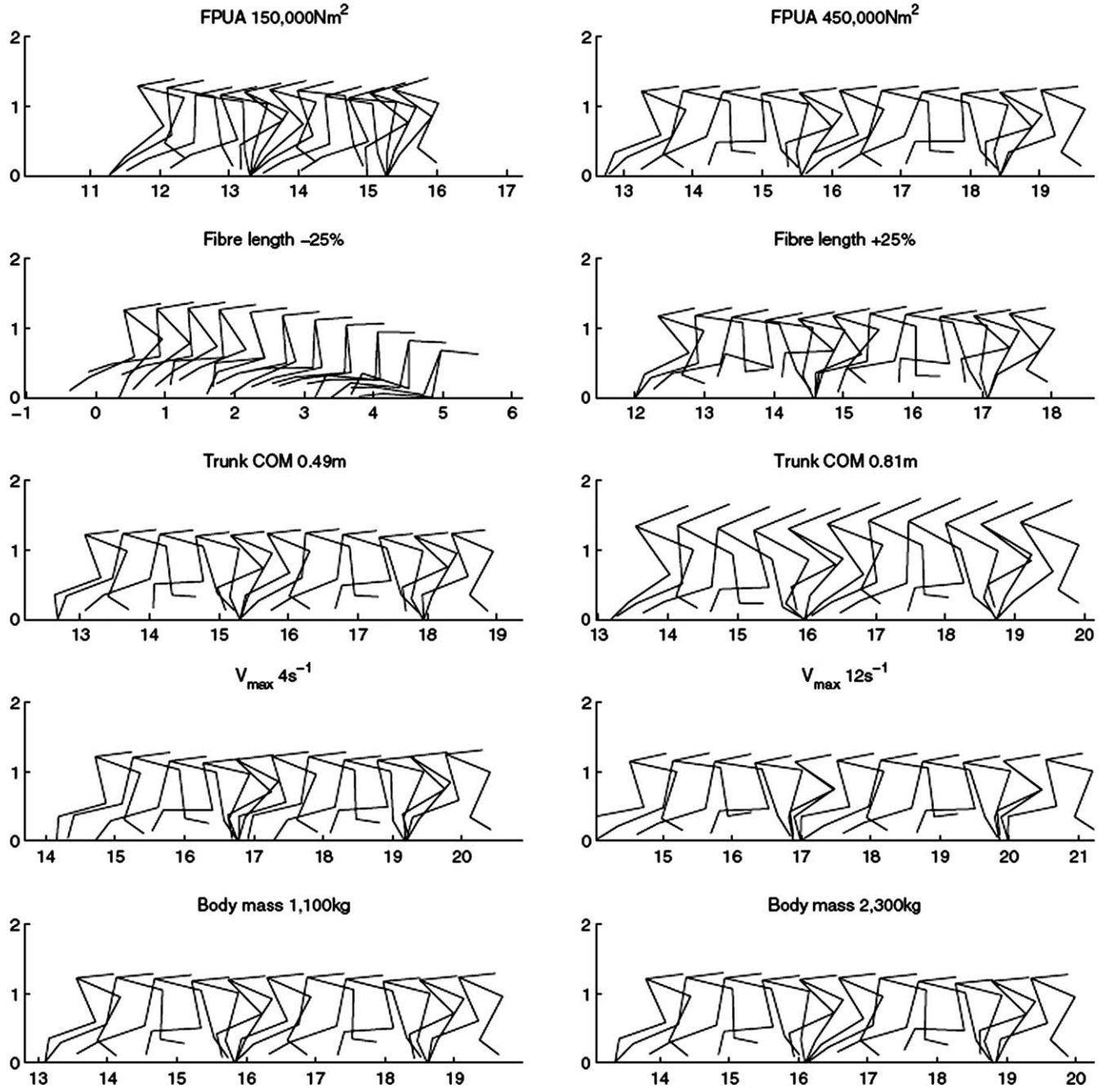

FIGURE 2. Overlay images of the best gait solutions for the minimum and maximum values of **A**, FPUA, **B**, fiber length, **C**, trunk CM, **D**, V_{max}, and **E**, body mass for *Allosaurus* in the OAAT sensitivity analysis. Stable running gaits (Froude number >1.5 with an aerial phase) were achieved for the full range of V_{max}, body mass, and trunk CM values. Stable locomotion was achieved with the increased fiber lengths tested, but could not be achieved when fiber lengths were lowered by 20% or more. All scales are in meters and 11 images are generated per gait cycle.

Predicted top speed ranged from 4.5 m/s with FPUA at 150,000 Nm^{-2} to 10.7 m/s at an FPUA of 450,000 Nm^{-2}, equating to 65.9% variation about the best-estimate speed of 9.4 m/s (Sellers and Manning, 2007). Despite the significant range in tested values, body mass and trunk CM have virtually no effect on the predicted top speed (Fig. 3). Predicted stride lengths show a similar pattern of distribution to maximum speed, with FPUA, V_{max}, and fiber length having an approximately linear effect (Fig. 4A). FPUA again produces the greatest range in predicted values (Fig. 4B), yielding a minimum stride length of 4 m at low FPUA values and a maximum of 5.8 m at high values. Body mass and trunk CM have little effect over the range of values tested (Fig. 4).

DISCUSSION

Theoretical Consideration of Input Effects

The relationship between each input parameter and maximum running speed in the OAAT sensitivity analysis corresponds with

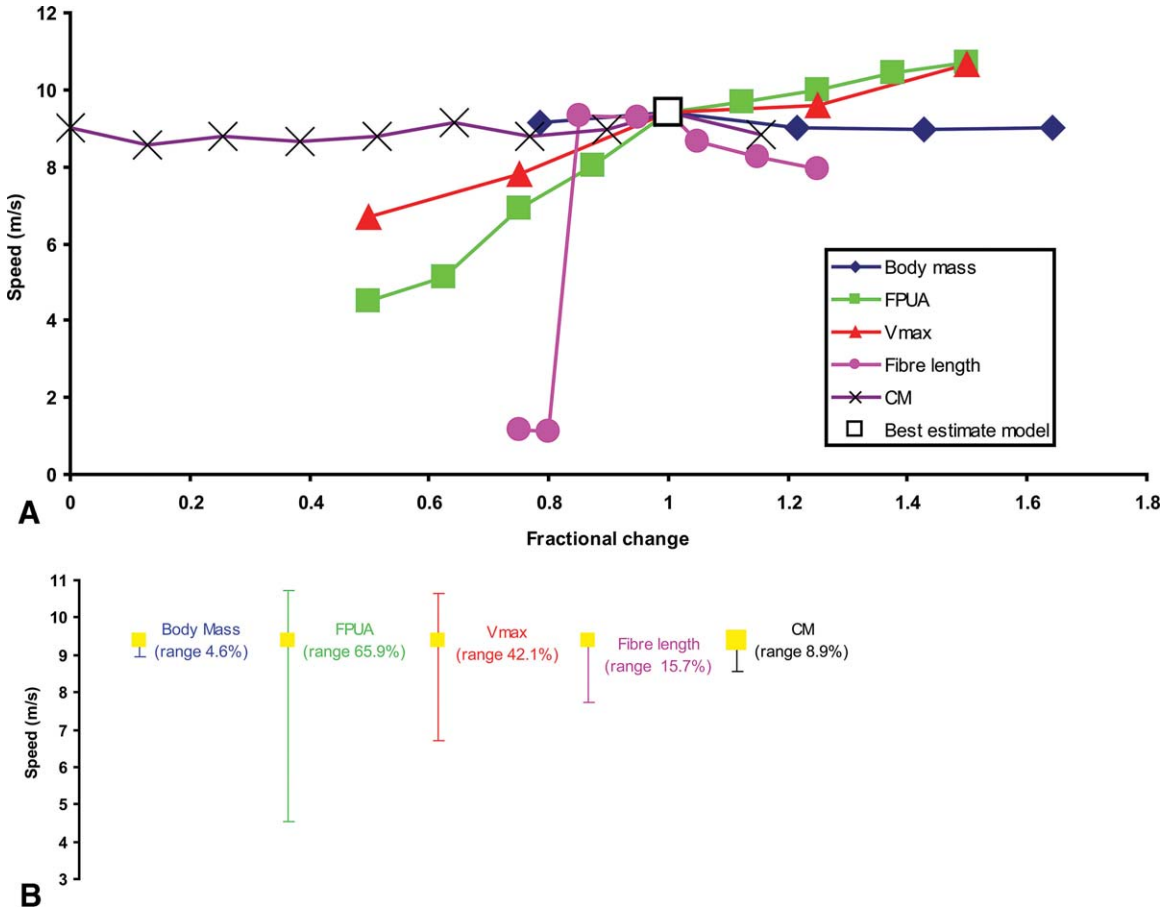

FIGURE 3. **A**, Fractional changes of input parameters plotted against maximum running speed for *Allosaurus.* **B**, Total range in maximum running speed about the best-estimate model value for each parameter in OAAT sensitivity analysis.

theoretical predictions (but see discussion of body mass effects below). Increasing FPUA and V_{max} and decreasing fiber length directly increases the maximum force and power each contracting muscle is able to generate, hence producing higher top speeds (Fig. 3). Increasing total body mass produces a larger yet geometrically similar model of *Allosaurus*, with an identical muscle mass:total body mass ratio with skeletal parameters unchanged. Hence predicted maximum running speed remains almost constant (Fig. 3). The minor amount of variation reflects the stochastic nature of the GA optimisation. The lack of effect resulting from changes in body mass is actually surprising. Simple geometrical models of top speed scaling (Hill, 1950) predict no effect of body mass, but this assumes concurrent changes in leg length scaling as mass$^{1/3}$, which is not occurring in the model used in this study. This lack of effect may be because over the limited mass range used, the leg scaling would have been rather small so its effect cannot be seen. It is also likely that the simple geometric model does not accurately predict running speed (Blanco and Gambini, 2007) and this is reflected in these results. In this analysis, no consideration was given to skeletal loading, which may severely restrict the ability to attain high speeds at the largest body masses tested. There is no theoretical reason why, in such a simple model, trunk CM should influence maximum running speed within its appropriate functional range, which is defined as the point at which the foot is no longer able to attain a position forward of the trunk CM in order to produce the necessary ground reaction force (GRF) vector for forward propulsion. This limit was not exceeded by the range of trunk CM values tested, hence predicted maximum running speeds remained relatively constant with minor variation again attributable to the stochastic nature of the optimization technique.

Implications for the Prediction of Maximum Running Speed in Dinosaurs

FPUA (or its linear equivalents: muscle mass and physiological cross-sectional area) and V_{max} are shown to have the greatest effect on top speed (Fig. 3) and therefore represent the major source of uncertainty in running speed predictions for extinct dinosaurs. The broad range in FPUA and V_{max} values available in the literature reflects the highly variable contractile properties of vertebrate muscle, both within muscle groups and between individual species. Values for FPUA included 200,000 Nm^{-2} for fish (Weatneat, 2003), 250,000 Nm^{-2} (Umberger et al., 2003) and 350,000 Nm^{-2} (Pierrynowski, 1995) for humans, 330,000 Nm^{-2} for cat, and 360,000 Nm^{-2} for frog parallel fibered leg muscles (Alexander, 2003), and a value of 400,000 Nm^{-2} for human quadriceps (Zheng et al., 1998). There is a similarly large range for V_{max}, with values highly dependent both on the fiber-type composition of the muscle and on the temperature. Winter (1990) suggests values from 6 to 10 times the muscle's resting length per second for humans. Westneat (2003) reported a range of values for fish from 3 to 10 s^{-1} for different fiber types and Umberger et al. (2003) recommended values of

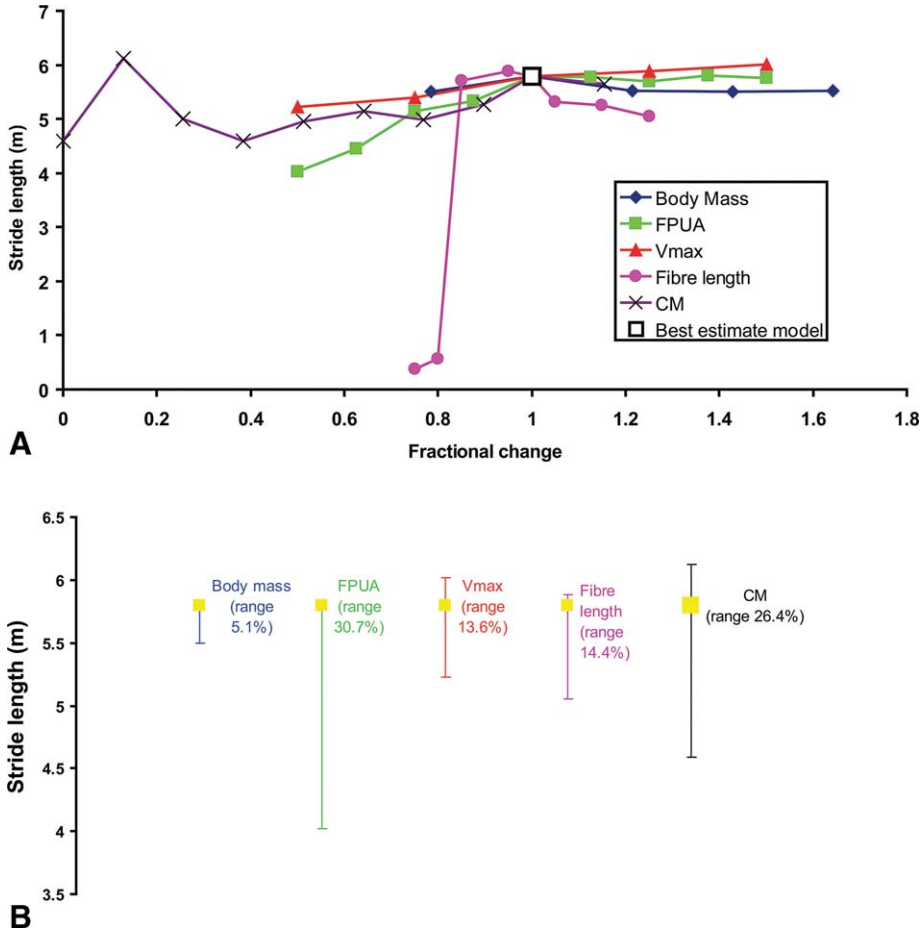

FIGURE 4. **A**, Fractional changes of input parameters plotted against stride length for *Allosaurus*. **B**, Total range in stride length about the best-estimate model value for each parameter in OAAT sensitivity analysis.

12 s^{-1} for fast-twitch and 4.8 s^{-1} for slow-twitch fibers. Although these ranges currently appear broad, the majority of data points do cluster around the overall mean value (particularly for the larger terrestrial animals tested), allowing sensible best-estimate values to be chosen for these parameters. However, values for total hind limb muscle mass (linearly equivalent to FPUA in our model) in non-avian dinosaurs are poorly constrained and the cause of significant debate (Hutchinson and Garcia, 2002; Paul, 1988, 2008; Hutchinson et al., 2007; Bates et al., 2009a). The lack of phylogenetic and functional analogues for large (>1000 kg) bipedal dinosaurs is confounded further by a lack of muscle mass data from extant taxa, with only a handful of published values for the ratio of hind limb muscle mass to total body mass in living bipeds. In most studies of extant species, complete limb segments are weighed so that bone mass is included muscle mass measurements, whereas in other cases the body mass of the dissected specimen is not stated and thus ratio of 'locomotor muscle mass' to total body mass cannot be determined. However, these former studies do provide a proxy for limb muscle mass to total body mass ratio in extant bipeds. The eight habitual bipeds studied by Hutchinson (2004a) had total hind limb masses (both limbs combined) equivalent to 18.5–54.6% total body mass, whereas data on the black-billed magpie (*Pica pica*) suggests 18% represents an average for this species (Verstappen et al., 1998). Smith et al. (2006) dissected the complete musculature of the pelvic limbs of 10 ostrich (*Struthio camelus*) and found the mean total muscle mass (both legs combined) to be 33.7% ± 2.1% total body mass. The best-estimate *Allosaurus* (Sellers and Manning, 2007) had 47.7% total body mass in both limbs combined, which falls within this range. The equation for muscle force in the simulator is such that the minimum and maximum muscle FPUA area values tested (150,000 and 450,000 Nm^{-2}) are equivalent to models of *Allosaurus* with hind limb muscle masses in both limbs at 23.86% and 67.56% of total body mass, respectively. This range exceeds that found in the literature for extant bipeds, including the highest values for extant ratites (Smith et al., 2006). Although some of these measurements are inclusive of bone mass, it is expected that extant ratites have higher hind limb mass to total mass ratios than non-avian dinosaurs given their relatively larger pelvic limbs, more slender thorax, and extensive air sac systems (Hutchinson et al., 2007).

Muscle fascicle lengths and other aspects of muscle architecture represent the most uncertain input parameters in models of extinct species and it is significant in terms of confidence that its effects are outweighed by other parameters. The EPB provided by crocodilians and crown-group birds offers a systematic means to estimate fascicle lengths in extinct dinosaurs on the basis of homology and in some cases functional considerations (Hutchinson, 2004b). A linear relationship between fiber length and muscle force (hence top speed) was borne out by our simple model of *Allosaurus*, but its effect is likely to be more complex in more detailed models with multiple muscles crossing hind limb joints.

Body mass and trunk CM had no effect on performance predictions despite the extremely broad range of values tested for both parameters. Sensitivity analysis on a volumetric reconstruction of the most complete specimen of *Allosaurus* currently known (MOR 693) indicates that the 'plausible' range for both total

body mass values lies well within the range tested here for an *Allosaurus* with skeletal proportions similar to the model used here (Bates et al., 2009b). This study suggested that the trunk CM was likely to have been between 7% and 64% of femoral length cranial of the hip joint in *Allosaurus* (Bates et al., 2009b). Altering trunk CM across this range resulted in little change to maximum speed, but it did affect the kinematics of limbs and torso in running gaits owing to the sub-horizontal orientation of the torso in bipedal non-avian theropod dinosaurs. Specifically, under more craniad trunk CM positions, the model tended to respond by increasing the angle of the trunk with respect to the ground, such that the anterior half of the body becomes raised to limit the excursion of the CM away from the hip joint on the longitudinal axis (Fig. 2C). Clearly a more anatomically realistic trunk model is required to fully constrain the effects of trunk CM position on locomotor performance, particularly if meaningful kinematic predictions are to be made.

There is significant scope to extend this sensitivity to investigate the effects of other parameters on performance predictions, notably the location of ligament and tendon attachments and the values for elastic parameters. Performance predictions would also benefit from greater bio-fidelity in the anatomical model. The model could be 3D and include more muscles, including two joint muscles and other soft tissues (e.g., ligaments). Improved realism in the trunk may also help constrain or bracket the functional range of trunk CM values for bipedal dinosaurs.

Speed Predictions and Higher-Level Interpretations

The significant effect of muscle parameters on predicted top speed clearly has a profound effect on any secondary higher-level interpretations of the behavioral ecology of *Allosaurus*. Maximum running speed is an important determinant of ecological behavior and success in terrestrial vertebrates, and plays a fundamental role in predator-prey interactions (Alexander, 2003). Indeed, as the effects of these parameters almost certainly apply equally to potential prey species and other aspects of their locomotor ability, such as acceleration and turning (e.g., Hutchinson et al., 2007), the current range in plausible values for soft tissue properties makes a robust quantitative assessment of behavioral ecology and species interactions in dinosaurian communities extremely difficult. Furthermore, the effects identified here for individual parameters are likely to be exacerbated if multiple factors, particularly FPUA and V_{max}, are similarly over- or underestimated. There is almost certainly interaction between these parameters, which could be explored using a full Monte Carlo analysis (Campolongo et al., 2000). In such an analysis, all the muscle parameters (FPUA, muscle mass, fiber length, V_{max}) would all be included so their individual uncertainties and interactions could be assessed. However, this is currently impractical due to the computational expense of such an analysis.

The present inability to tightly constrain the ranges of soft tissue input values raises the question of whether any estimation of maximum running speed is currently reliable enough for higher-level inferences to be based upon. It is important to emphasize that best-estimate values are chosen because they are considered to have the highest probability of matching correct values based on our current knowledge of vertebrate skeletal muscle and dinosaur soft tissue anatomy (Table 1). Values at the extreme of ranges therefore represent the most unlikely values for each parameter. Although it is likely that precise values for muscle parameters will never be obtained for extinct dinosaurs, more work on locomotor muscle physiology of extant vertebrates, and particularly large animals, will allow these ranges to be constrained further. In addition, it may be possible to constrain muscle parameters based on skeletal safety factors: although it is possible to postulate very large muscle mass or high contractile forces, these are only plausible if the skeleton is strong enough to withstand the forces generated. Similarly, muscles must be able to generate the forces required for a minimal locomotor repertoire: walking, standing, getting up from the ground and this provides a functional lower limit. However in spite of the present uncertainty about numerous input values, our approach allows us to disprove certain hypotheses regarding locomotor performance in extinct animals. In particular, this sensitivity analysis has shown that even with high hind limb muscle masses or maximized contractile properties, large bipedal dinosaurs could not have obtained the high speeds (>20 m/s) postulated by some workers (Bakker, 1986; Paul, 1988, 1998). Indeed, this sensitivity analysis suggests that speeds in excess of 12 m/s require not only high relative muscle masses compared to those known for extant bipeds, but also muscle-tendon properties highly optimized for fast running. Higher speeds for *Allosaurus* (and by inference similarly proportioned theropods) are therefore unlikely based on current simulations. In future studies, the range in speed predictions will be further refined by more anatomically realistic models.

CONCLUSION

Sensitivity analysis provides a means to quantify the effects of poorly understood input parameters in dynamic simulations of locomotion and in biomechanical modeling in general. In particular, certain values for soft tissue parameters are tenuously estimable in extinct animals and sensitivity analysis offers an understanding of how variation in and between these parameters may interact to produce functional outcomes. This study of *Allosaurus* has shown that soft tissue parameters tested (FPUA, V_{max}, and fiber length) have an approximately linear effect on performance predictions, in accordance with theoretical predictions. FPUA has the greatest effect on the simulated gait across the range observed in extant taxa, equating to 65.9% variation in speed (4.5–10.7 m/s) and 30.7% variation in stride length about the original best-estimate model predictions of 9.4 m/s and 5.8 m (Sellers and Manning, 2007). Body mass and trunk CM had no effect on performance predictions over the range of values tested, suggesting existing values for these parameters are accurate enough for performance predictions. However, future analyses that aim to reverse engineer the locomotor kinematics of extinct dinosaurs will have to consider the impact of trunk CM, which significantly affected limb kinematics and torso orientation in *Allosaurus*. Mass reconstructions of dinosaurs should routinely include a sensitivity analysis (e.g., Hutchinson et al., 2007; Bates et al., 2009a) to provide plausible ranges of trunk CM for dynamic biomechanical simulations. A more complete quantitative understanding of the relationship between body mass and locomotor capability might be achieved by consideration of skeletal loading in future models. The range in possible gaits produced in this OAAT sensitivity analyses emphasises the current limitations in the predictive power of biomechanical techniques that result from an inability to extract soft tissue characteristics from the fossil record. More work on the hind limb muscle physiology of extant terrestrial vertebrates, particularly larger species, is required to constrain the current range of input values and subsequently the array of plausible gaits for extinct species. The uncertainty inherent in current biomechanical predictions must be taken into account when considering paleoecological and evolutionary hypotheses. However, the facility to conduct controlled repeatable experiments in the form of sensitivity analyses means that the effects of such uncertainties can be quantitatively tested and in many cases enable higher-level interpretations to be appropriately constrained.

ACKNOWLEDGMENTS

This research was funded by grants from BBSRC, National Environmental Research Council, and the Leverhulme Trust to W.I.S., a National Environmental Research Council grant to

K.T.B., and the HECToR project e72, EP/F055595/1, funded through the HECToR Capability Challenge Call to L.M.. The authors would like to thank the editors, Mark Wilson, Robert Reisz, and David Weishampel for their patience and hard work on this paper during the submission process, and the two reviewers, Eric Snively and Roger Benson, for helpful suggestions that greatly improved the manuscript.

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Submitted October 31, 2008; accepted March 14, 2009.